

Linking Locust Gregarization to Local Resource Distribution Patterns Across a Large Spatial Scale

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ABSTRACT Spatial resource distribution patterns play an important role in mediating density-dependent phase change (gregarization) in locusts. The degree of contagion or aggregation of resources in a habitat can increase the probability of locust gregarization by increasing the frequency of contact among individual locusts. The spatial distribution patterns of two resources upon which gregarization can occur, the tussock grasses *Aristida pungens* and *Panicum turgidum* (Poaceae), were examined in two adjacent regions of the desert locust (*Schistocerca gregaria* Forskål) plague recession area in Mauritania that differ in their frequencies of locust gregarization. The hypothesis that the distribution of grass tufts should be more aggregated and thus more likely to promote locust phase change in the high frequency gregarization area was tested. Tufts were more abundant, and both species were larger in the high frequency gregarization area. The spatial distribution patterns of tufts in both areas were largely aggregated at the 200- to 2000-m² scale corresponding to the population-level scale of locust resources. As predicted, the degree of aggregation was more extreme across the high frequency gregarization area. This study provides support across a large area for the predicted association between local resource distribution and locust gregarization. The observed differences in grass abundance and size between the high and low frequency gregarization areas suggest that factors such as topography or hydrology may underlie differences in plant distribution and contribute to locust gregarization in the high frequency area.

KEY WORDS *Schistocerca gregaria*, phase, aggregation, gregarization

LOCUST SPECIES SUCH as the desert locust, *Schistocerca gregaria* Forskål (Orthoptera: Acrididae), exhibit phase polyphenism, a type of phenotypic plasticity in which the expression of an array of behavioral, physiological, and morphological traits can be influenced by changes in local population density (Uvarov 1966, Pener 1991, Pener and Yerushalmi 1998). The process of phase transformation whereby low density solitary phase individuals change into the high density gregarious phase is often referred to as gregarization. Behavior is among the first traits to change during gregarization, and these changes play an important role in swarm formation (Simpson et al. 1999 and references therein). The simultaneous expression of increased activity and mutual attraction among gregarious phase locusts presumably leads to the formation of large cohesive bands of nymphs and flying swarms of adults (Uvarov 1977). Behavioral gregarization also increases the contact rate among individuals and promotes density-dependent changes in other traits (Despland and Simpson 2000b). Some of these

changes, such as the expression of density-dependent pathogen resistance and density-dependent warning coloration, may further contribute to the outbreak process by reducing locust mortality (Sword et al. 2000, Sword and Simpson 2000, Wilson et al. 2002).

As local population densities increase, the underlying pattern of resource distribution can play a critical role in either promoting or deterring locust gregarization (Kennedy 1939, Ellis 1963). Behavioral phase change is mediated primarily by direct tactile contact among individuals (Roessingh et al. 1998, Hägele and Simpson 2000, Simpson et al. 2001) and can be transmitted across generations via epigenetic effects (Islam et al. 1994a, b; McCaffery et al. 1998; Hägele et al. 2000; Bouaïchi and Simpson 2003). Solitary phase locusts are initially repelled by the presence of other locusts. However, they are more likely to come into contact with others and subsequently gregarize when the resources they use, such as host plants, roosting, or oviposition sites, are distributed in an aggregated (contagious) pattern. Thus, at a given population density, locust gregarization is more likely to occur within as well as across generations in habitats in which resources are distributed in an aggregated manner (Ellis 1963, Bouaïchi et al. 1996, Collett et al. 1998, Despland et al. 2000, Despland and Simpson

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2000a, b). As a result, knowledge of the spatial distribution of resources could be very important for locust management by aiding in the identification of habitats that are likely to promote locust gregarization (Collett et al. 1998).

Locust survey data from 1988 to 1999 collected by the Centre de Lutte Antiacridienne in Mauritania as part of its preventative management strategy (Ould Babah 1997) have identified a specific region in the center of the country where transiens phase juvenile desert locusts occur at unusually high frequencies relative to other areas. The transiens phase is an intermediate phenotypic state of locusts between the low density solitary and high density gregarious phases (Uvarov 1966). The transiens phase juveniles found in the high frequency area may have been the progeny of gregarious phase locusts that were undergoing phase transformation toward the solitary phase at the time of sampling. This is unlikely, however, because gregarious phase populations and swarms were relatively rare in this region during the analyzed plague recession period. The more plausible explanation is that the high frequency of transiens phase locusts in this region was indicative of frequent local gregarization. This is further supported by the presence of primarily nongregarious locust populations in this region relative to other areas of the country during the plague recession period of 1964–1987 (Popov 1992). The elucidation of regions in Mauritania that differ in the frequency of locust gregarization provides an opportunity to compare ecological characteristics that can affect locust population growth and gregarization between the high and adjacent low frequency areas.

In light of the known association between local patterns of resource distribution and locust gregarization, the spatial distributions of two perennial tussock grasses, *Panicum turgidum* Forsk. and *Aristida pungens* Desf. (sometimes referred to as *Stipagrostis pungens*) (Poaceae) (Ozenda 1991), were examined. These grasses are numerically dominant throughout the study area and thought to be important resources upon which contact among locusts and subsequent gregarization can occur. Specifically, the hypothesis tested was that the distribution of grass tufts should be more aggregated and therefore more likely to promote locust phase change in the high frequency gregarization area.

Materials and Methods

Study Areas. The region of central Mauritania containing the low and adjacent high frequency gregarization study sites is located in the eastern and southeastern parts of Aouker Lebken and the western part of the Mauritanide mountain chain. It lies at the intersection of four administrative regions, Adrar, Tagant, Brakna, and Inchiri. The area is a vast alluvial plain with a variety of cover types including freestanding dunes, fields of mobile dunes (barkanes), and large chains of dunes. Some local drainages give rise to saline depressions (sebkhas) in its northern limits, and

there are occasional outcrops of rock on the surface, sometimes surrounded by eroded rings. Currently, wind erosion is shaping the superficial substrata into patterns reflecting the prevailing wind conditions.

The area is very difficult to access and has no permanent human population or wells. Nomads bring their animals into the area only during the cool rainy season or when there are no other alternatives. The temperature can reach $>45^{\circ}\text{C}$ in the summer and drop to $\approx 10^{\circ}\text{C}$ during winter nights. The nearest permanent meteorological station is 150 km from the study sites in Tidjikja ($18^{\circ} 34'\text{N}$, $11^{\circ} 26'\text{W}$). The annual vegetation after rain can remain green until January and is mainly composed of *Tribulus macropterus* (Boiss.) (Zygophyllaceae), *Boerhavia repens* L. (Nyctaginaceae), *Farsetia stylosa* R. Br. (Brassicaceae), *Cyperus conglomeratus* Rottb. (Cyperaceae), *Heliotropium ramosissimum* (Lehm.) DC. (Boraginaceae), and *Aristida plumosa* L. (Poaceae). The dominant perennials are *Aristida pungens* Desf. and *Panicum turgidum* Forsk. (Poaceae). Other very rare perennials include *Acacia tortillis* Forsk. (Leguminosae), *Capparis decidua* (Forsk.) Edgew., *Maerua crassifolia* Forsk., and *Boscia senegalensis* (Pers.) Lam. ex Poir. (Capparidaceae).

The low frequency gregarization area was defined as a quarter degree square ($18^{\circ} 30'\text{N}$ to $19^{\circ} 00'\text{N}$ and $13^{\circ} 00'\text{W}$ to $13^{\circ} 30'\text{W}$) of $\approx 250 \text{ km}^2$. The high frequency gregarization area was a similar quarter degree square bordering on the southeast corner of the low frequency area ($18^{\circ} 00'\text{N}$ to $18^{\circ} 30'\text{N}$ and $12^{\circ} 30'\text{W}$ to $13^{\circ} 00'\text{W}$). Navigation to and within the study sites was done with the assistance of a Trimble DGPS system.

Locust Resources. The spatial distributions of two tussock grasses, *P. turgidum* and *A. pungens*, were quantified. Tussock grasses, also known as bunch grasses, are commonly used as roost sites and serve to concentrate locusts in both low and high density populations. Locusts can accumulate in large numbers on tufts in the morning, midday, and night for thermoregulation and protection from predators (Kennedy 1939, Burnett 1951, Chapman 1955, Culmsee 2002). The perennial life history of these grasses also facilitates their use as indicators of longer-term environmental factors such as water availability that might influence locust population growth. In addition, as perennials they are amenable to sampling across a large area because, unlike annuals, their immediate presence or absence at a given location is independent of recent local rainfall.

Sampling Regime. Forty belt transects ($1 \text{ km} \times 2 \text{ m}$) were conducted within each of the high and low frequency gregarization areas. Each belt transect was divided into 10 contiguous quadrats ($100 \times 2 \text{ m}$). The number of *A. pungens* and *P. turgidum* tufts present in each quadrat was recorded. Transects were sampled from a 4×4 vehicle while en route from Nouakchott, Mauritania, to recently erected weather stations maintained in the experimental plots. Twenty of the 40 transects in each area were conducted in October, and the remaining 20 per area in November of 2002. Within each area, 1 set of 20 transects was conducted along an

east-west heading, and the other along a nonoverlapping north-south heading. The starting point of each transect was haphazardly chosen by a passenger in the rear of the vehicle, and individual transects did not overlap. Transect width was visualized as 2 m perpendicular to the passenger side door. Quadrat and transect length were determined using the vehicle's odometer. Transects were driven as straight as possible, with deviations only to ensure safe passage of the vehicle through rough terrain. Extensive and impassable dune systems, devoid of vegetation, were necessarily avoided.

While conducting the belt transects in each of the areas, plant sizes were sampled using 20 additional line transects established at randomly selected points along the course of travel. Each transect was randomly oriented and 300 m maximum length. The transects were walked from the starting point, and the maximum diameter and height of the first 10 *A. pungens* and 10 *P. turgidum* tufts encountered, if present, were measured.

Analysis. This experiment was designed as a comparative mensurative experiment in which measurements were dispersed in space within the high and low frequency gregarization areas (i.e., treatments), and can be considered true replicates (Hurlbert 1984). We compared tuft abundance per transect, maximum diameter, and maximum height, of each grass species between the low and high frequency areas. The two grass species co-occurred in many transects and are similar in structure. Because locusts may use tufts of both species as a single resource and not distinguish between them as taxonomic units, the total abundance of tufts per transect was also compared between the areas. Comparisons of abundance per transect, plant diameter, and plant height between the low and high frequency gregarization areas were made with independent sample *t* tests controlled if necessary for inequality of variances, as determined by Levene's test in SPSS 11.0.1 (SPSS 1999).

The spatial distribution patterns of tufts of each grass species as well as both resources combined were quantified within each 2000-m² belt transect using the standardized Morisita index of dispersion (I_p) (Smith-Gill 1975, Krebs 1999). The I_p varies from -1.0 to +1.0 with zero values suggesting a random distribution. Negative values indicate uniformity, and positive values indicate an aggregated distribution pattern. The 95% confidence intervals for a departure from random toward either uniformity or aggregation are given by values of -0.5 and +0.5, respectively. The standardized Morisita index is considered one of the best measures of dispersion because it is independent of population density and sample size (Myers 1978, Krebs 1999). These qualities facilitate its use in comparing patterns of distribution among populations with different sample sizes.

For each grass species as well as both resources combined, the number of transects having either uniform, random, or aggregated distributions as determined by their I_p values were compared between the high and low frequency areas with a permutation-

based Monte Carlo $R \times C$ contingency table analysis (50,000 iterations) (available at <http://engels.genetics.wisc.edu/pstat/>) to account for cells with values less than 5 (Zar 1999). In addition to comparing the relative frequencies of each distribution type between the two areas, differences in the relative magnitude and variability of local resource aggregation between the areas were also examined. These comparisons were made using independent sample *t* tests and Levene's tests for inequality of variance on I_p values for each species separately and the two resources considered together.

Results

There were significant differences in both grass tuft abundance and size between the high and low frequency gregarization areas. Tuft abundances per transect were significantly greater in the high frequency area for *P. turgidum*, and both species considered together as a single resource (*P. turgidum*, $t = 4.22$, $df = 51.308$, $P < 0.001$; *A. pungens*, $t = 0.506$, $df = 66$, $P = 0.615$; combined, $t = 6.058$, $df = 63.877$, $P < 0.001$) (Fig. 1). In terms of size, *A. pungens* tufts were significantly larger in diameter ($t = 4.652$, $df = 315.4$, $P < 0.001$), and *P. turgidum* tufts were significantly taller ($t = 2.185$, $df = 26$, $P = 0.03$) in the high frequency area (Fig. 2).

The patterns of grass tuft spatial distribution differed between the high and low frequency gregarization areas as well. Standardized Morisita index of dispersion (I_p) values calculated for each transect indicated that tuft distribution patterns of *A. pungens* and both resources combined were significantly more likely to be aggregated, as opposed to random or uniform, in the high frequency area (Table 1). *P. turgidum* exhibited a similar trend, but the difference was not significant (Table 1). In addition to being aggregated more often, Levene's tests for equality of variance on I_p values between the areas for each resource type revealed that tuft distribution patterns were significantly less variable in the high frequency area (*P. turgidum*, $F = 22.677$; $df = 1, 59$; $P < 0.001$; *A. pungens*, $F = 68.185$; $df = 1, 67$; $P < 0.001$; combined, $F = 100.098$; $df = 1, 78$; $P < 0.001$). Overall, the relative degree of resource aggregation was greater in the high frequency gregarization area as determined by comparisons of I_p values between areas for each resource type (*P. turgidum*, $t = 1.873$, $df = 24.508$, $P = 0.073$; *A. pungens*, $t = 3.489$, $df = 48.336$, $P = 0.001$; combined, $t = 3.655$, $df = 44.552$, $P = 0.001$) (Fig. 3).

Discussion

The spatial distribution patterns of two dominant tussock grass species, resources upon which locust contact and gregarization can occur, tend to be locally aggregated to a greater extent in a region of Mauritania with a high frequency of locust gregarization. These findings are consistent with the empirically demonstrated relationship between local resource distribution patterns and locust gregarization. Previous labo-

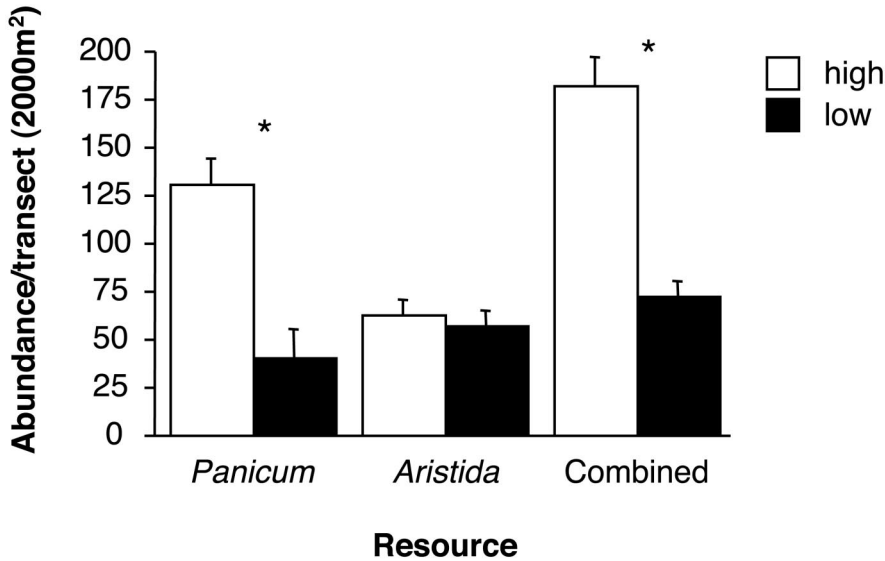


Fig. 1. Mean (\pm SE) grass tuft abundance per transect of *P. turgidum* ($n = 60$), *A. pungens* ($n = 68$), and both resources combined ($n = 79$) in high and low frequency gregarization areas of the desert locust in Mauritania. *, $P < 0.001$.

ratory and field studies have generally considered the effects of local resource distribution on gregarization within a single population (e.g., Ellis 1963; Bouaïchi et al. 1996; Collett et al. 1998; Despland et al. 2000; Despland and Simpson 2000a, b; Despland 2003). This study expanded this concept to a larger spatial scale by sampling local resource distribution patterns in a number of potential locust habitats across a large area. In doing so, the predicted association between increased local aggregation of resources and increased probability of locust gregarization was found to hold true (Table 1; Fig. 3).

Although the predicted relationship was observed, a causal relationship between resource distribution

and locust gregarization was not directly demonstrated in this study. It is important to note that the observed higher abundance of resources in the high frequency area (Fig. 1) could potentially act to decrease gregarization by reducing contact among individuals (Despland et al. 2000, Despland 2003). However, at a larger spatial scale, the higher abundance of resources in the high frequency area could positively influence locust gregarization by promoting immigration from outlying areas (Despland et al. 2004). This was not a manipulative field experiment, but rather an attempt to link the well-studied relationship between local resource distribution and individual locust behavior to larger-scale and longer-term patterns ob-

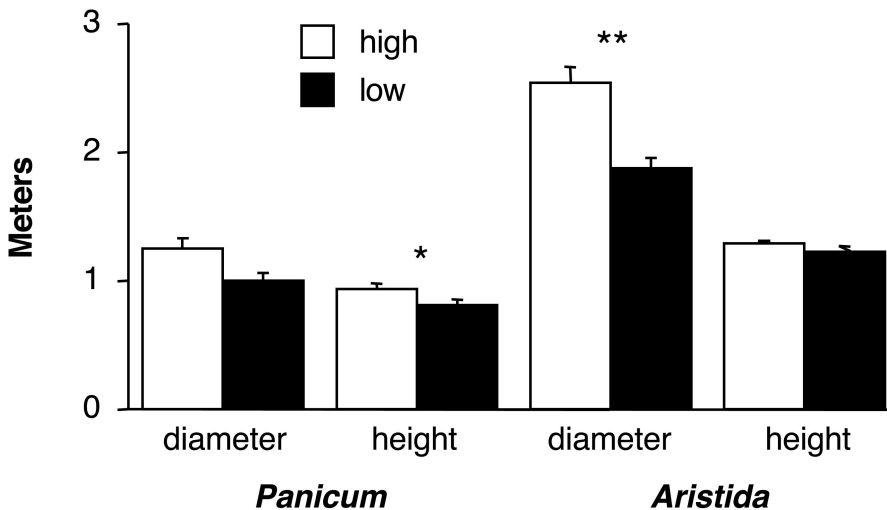


Fig. 2. Mean (\pm SE) maximum diameter and height of *P. turgidum* ($n = 267$) and *A. pungens* ($n = 351$) tufts in high and low frequency gregarization areas of the desert locust in Mauritania. *, $P < 0.05$; **, $P < 0.001$.

Table 1. The spatial distributions of tufts of *P. turgidum*, *A. pungens*, and both resources combined in high and low frequency gregarization areas of the desert locust in Mauritania

Plant	Zone	% transects	Uniform	Random	Aggregated	P
<i>P. turgidum</i>	High	100 (40/40)	1	2	37	0.079
	Low	50 (20/40)	2	5	13	
<i>A. pungens</i>	High	82.5 (33/40)	1	2	30	0.001
	Low	85 (35/40)	6	9	20	
Combined	High	100 (40/40)	0	6	34	0.002
	Low	92.5 (39/40)	6	12	21	

Spatial distribution patterns were determined using the standardized Morisita index of dispersion (I_p) (Krebs, 1999) calculated for each 1 km \times 2-m belt transect. Differences in the frequency of distribution patterns between the high and low frequency areas for each plant as well as the overall resource base were compared with a permutation-based Monte Carlo contingency table analysis.

served in the field. The larger goal of explaining precisely why gregarization has been more frequent over time in the high frequency area will be a much more complicated endeavor. Studies of some of the other factors that may further contribute to understanding the difference in gregarization frequency between the two areas such as weather, topography, hydrology, soil type, plant community composition, and predator abundance are planned or ongoing.

Quantifying the spatial distribution patterns of organisms in a habitat does not inherently provide an understanding of the ecological mechanisms that determine their distributions (Krebs 1999). Our data in conjunction with field observations may provide clues as to why resources are more aggregated in the high frequency area. Clearly, rainfall is essential for locust population growth and subsequent gregarization because it enables host plant growth and suitable soil moisture for egg development. Unfortunately, long-term local weather data for these sites are not available. The centers of the studied low and high fre-

quency gregarization areas were only ≈ 100 km apart, and both fall within the 70–100 mm/yr rainfall isohyet. Neither is situated near mountain systems that might differentially influence precipitation. Therefore, it seems unlikely that rainfall amounts have differed appreciably between the two areas. Topographic relief, however, does appear to be more variable in the high frequency area. The low frequency area is relatively flat, with occasional relief provided primarily by highly mobile dunes. In contrast, the high frequency area is characterized by more abundant stable dune systems superimposed upon existing drainages. The variation in topography provided by these dunes creates a somewhat homogeneous succession of dunes and interdune depressions in which runoff from fleeting rainfall may collect, become available for plant growth, and potentially facilitate local locust reproduction, followed by gregarization. Our finding that resource distribution patterns in the high frequency gregarization area were more locally aggregated, but significantly less variable, seems to reflect the differ-

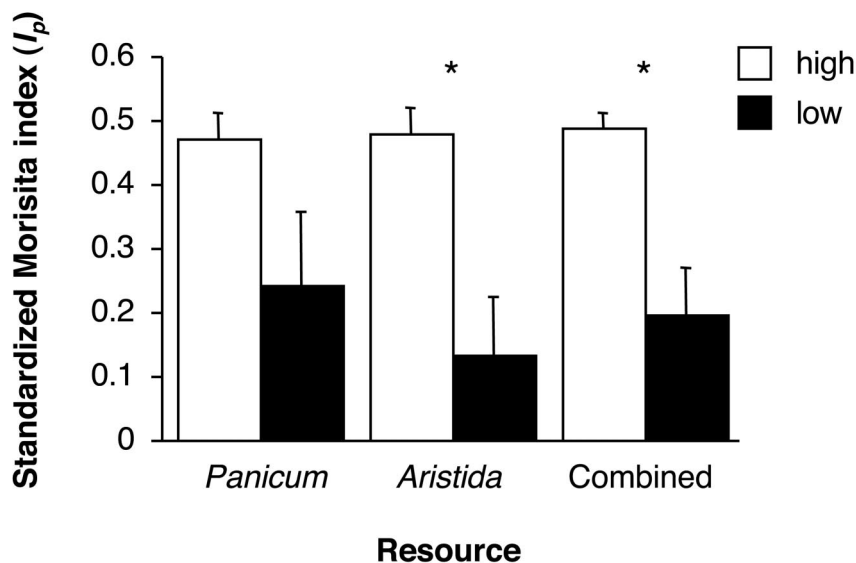


Fig. 3. Spatial distributions of *P. turgidum* ($n = 60$), *A. pungens* ($n = 68$), and both resources combined ($n = 79$) in high and low frequency gregarization areas of the desert locust in Mauritania. Bars represent mean (\pm SE) of the standardized Morisita index of dispersion (I_p) values calculated for each transect and resource type within each area. I_p values can range from +1 to -1, indicating aggregation versus uniformity, respectively. *, $P < 0.001$.

ences in topography that we observed between the two study areas. Similar, but larger scale, associations between topography, hydrology, and locust breeding have been noted in other parts of the desert locust recession area (Popov et al. 1984, Skaf et al. 1990).

Although a number of different factors can influence plant growth, tufts of *P. turgidum* and *A. pungens* tended to be larger in the high frequency area (Fig. 2), consistent with the possibility of greater water availability in these habitats. *P. turgidum* was also more abundant in the high frequency area (Fig. 1), suggesting that seedling germination and establishment, which requires the equivalent of at least 20–30 mm of rain (Migahid and El-Shourbagui 1958), were more successful over the long-term in the high frequency area. Additionally, it has been suggested that tussock grasses in West Africa increasingly space themselves apart from each other as water availability decreases (Williams and Farias 1971). This may account for the observed increase in random and uniform local distribution patterns among grass tufts observed in the low frequency area (Table 1). The sum of these observations suggests that topography and hydrology may interact to influence plant performance and their distributions by increasing the amount of water locally available in the high frequency area. Perhaps not surprisingly, this same interaction is also likely to generate a mosaic of habitats favorable for both locust reproduction and gregarization.

The scale at which ecological studies are conducted is one of the fundamental issues in ecology (Wiens 1989, Levin 1992). Desert locust population dynamics are still poorly understood (Collett et al. 1998), and an emerging trend has been a call for a better understanding of the local ecological mechanisms that underlie outbreaks and swarm formation (e.g., Joern and Gaines 1990, Bouaïchi et al. 1996, Collett et al. 1998, Sword et al. 2000). As such, sampling scale is clearly a critical consideration in linking locust gregarization to local ecological conditions. Local resource distribution in this study was quantified at a scale of 200–2000 m². This may arguably be too large of a scale when considering the effect of resource distribution on hatchlings whose movement among tufts is likely to occur in areas <200 m². However, aggregation of resources even at this scale could feasibly affect the oviposition behavior of females and the subsequent gregarization of their hatchlings. For more mobile latter instar juveniles as well as adults, the scale of resource distribution quantified in this study is certainly relevant in influencing the local distribution of individuals and mediating density-dependent changes in their behavior.

Local resource distribution data could feasibly be collected in a number of ways, including remote sensing and aerial photography. Despland et al. (2004) recently investigated use of satellite imagery to quantify locust resource distribution patterns. They found the technique to be limited by the quality of available data and concluded that ground-based survey of high-risk habitats, as was done in this study, is essential. There are also other techniques available for quanti-

fying resource distribution patterns, such as the use of fractal dimensions. Fractals have a number of desirable qualities that are useful for examinations of locust resource distribution (Despland 2003). As collected, the data presented in this study do not lend itself to the calculation of fractals to compare the relative merits of the two techniques. This study has, however, demonstrated that simple sampling approaches aimed at quantifying locust resource distribution patterns can be conducted with very little added cost or effort by locust survey teams already operating on the ground. Knowledge of local resource distribution patterns can enhance preventative locust management operations by aiding in the identification of habitats likely to promote locust swarm formation (Collett et al. 1998). Applying such an approach may facilitate more precise survey and control operations in locust-afflicted countries with concomitant reductions in financial costs, pesticide use, and potentially harmful effects on the environment.

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